

Notes on Rain-Forest Herbs

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Concise summaries of views on the herbaceous plants of rain-forest have been given by Richards (1952, pp. 96–102) and by Walter (1971, pp. 118–122). The present notes are an attempt to expand the subject a little further, by recording some observations on the growth patterns of dicotyledonous herbs and emphasising the contrasts both with monocotyledons and with temperate forest dicotyledons. At present the relation between structural features of the leaves and physiological function is, in general, rather uncertain, and this is not the field for a taxonomist to enter. Nevertheless I have ventured a few remarks, if only as a reminder of the questions a field-botanist wants to ask. These notes are inevitably limited by my personal experience, which wholly excludes the New World and is derived largely from collecting trips in Sarawak.

The importance of the massive tropical palms (Palmae) and screw-pines (Pandanaeae) in attaining a balanced appreciation of monocotyledons as a group is now widely recognized. But even at the level of rain-forest herbs a comparison between monocotyledons and dicotyledons illuminates some fundamental differences more brightly than a similar study in temperate forests. When these are brought into the picture, it is immediately apparent that, under the impact of a strongly seasonal climate, the contrast between monocotyledon and dicotyledon has been lessened.

First let us look at growth-habits, particularly at the underground parts. In temperate forests rhizomes or stolons with scale-leaves are frequent, both amongst dicotyledons and monocotyledons: for instance, *Mercurialis* (Euphorbiaceae — see Mukherji, 1936) or *Paris* (Liliaceae — see Kirchner, Loew & Schröter, 1934) in Europe; *Podophyllum* (Berberidaceae — see Holm, 1899) or *Medeola* (Liliaceae — see Bell, 1974) in North America. Examples could easily be multiplied.

Of the herbs of tropical rain-forest Richards (1952, p. 98) says “... plants with underground rhizomes are frequent, but the rhizomes are adapted for multiplication and migration rather than perennation”. He is echoed, despite a slightly different concept of perennation, by Walter (1971, p. 118): “the herbs are often equipped with underground perennating organs such as rhizomes and tubers. But these serve less as storage organs for reserve food than as a means of vegetative reproduction”. These statements need some qualification. They might seem to imply, no doubt unintentionally, that the rhizomes of temperate forest herbs do not serve for spread or vegetative reproduction; of course, they clearly do so. Secondly, in my experience, rhizomes may be common on tropical monocotyledons but they are certainly very rare amongst the dicotyledons. In considering rain-forest herbs the two groups *must* be distinguished.

It may be as well to restrict the words “storage” and “perennation” to use when a seasonal dormancy is accompanied by complete die-back of aerial shoots. Then the situation found in most non-seasonal rain-forest herbs with underground rhizomes may be described as the accumulation of food-reserves. The importance of this must not be underestimated in the monocotyledons. The rhizomes of many

Zingiberaceae eventually throw up massive new leaf-fronds anything from 1.5 to 9 metres in height. This can scarcely be achieved without the backing of some accumulated reserves, even though there is continuity through the rhizome or stolon to older actively photosynthetic fronds. Very often the tip of the rhizome becomes decidedly swollen when it turns up to form the new leaf-frond.

Some Zingiberaceae grow in tight clumps, and these, of course, have short slow-growing rhizomes; others form dense or diffuse patches, and in these the rhizome is extended as a far-ranging stolon. Apart from question of size, the patterns are those of rhizomatous herbs in temperate forests.

Dicotyledonous herbs also form patches in the rain-forest, but this is achieved without the aid of scale-clad underground rhizomes or stolons. A characteristic pattern of growth can be observed in *Cyrtandra radiculiflora* C.B.Cl. (Gesneriaceae). This species forms stands with erect leafy shoots keeping a more or less even height of about 0.75 metre. These shoots are evergreen and their duration is unknown. Flowering is axillary and basal, at or near ground level. The terminal bud remains vegetative and produces a succession of leaves. What prevents the shoots from growing higher and higher?

It seems that the average height is maintained because, as upwards growth proceeds, the lower part of the stem becomes more and more decumbent. If a handful of shoots are pulled up it will be found that they are linked by pieces of prostrate, sometimes buried, stem. Buds on the prostrate stems give rise to new shoots that help to thicken the patch, and the process of becoming prostrate helps to expand it. At all times the main growing points of the shoots are aerial and are directed upwards. There is no horizontal (diageotropic) growing point like that of a rhizome or stolon.

The pattern just described for *Cyrtandra radiculiflora* is found in a number of species of this genus (which is very large and very varied in growth-patterns), and in other genera where some species have axillary inflorescences: *Argostemma* (Rubiaceae), *Elatostema* (Urticaceae), *Linariantha* (Acanthaceae), *Gomphostemma* (Labiatae) come to mind. Other rain-forest herbs (e.g. some Acanthaceae) have terminal inflorescences; these plants retain their herbaceous stature by dying down to near the base after fruiting and form new shoots from basal buds: scars of old shoots are often visible, though I have never noticed a dead shoot in situ. Observations on the death-patterns of tropical herbs are badly needed: there are indications that the fruiting shoot may die slowly, so that its leaves are still photosynthetic long after the seeds are shed. This could be a necessary feature, in the absence of underground storage organs, to support the growth of a new shoot: but that is speculation until careful studies can be made. This pattern of growth is shown in some forest species of *Pseuderanthemum* (Acanthaceae); other members of the genus do not die back but produce shoot-buds from the axils of leaves just below the dead infructescence — and become shrubs. Another genus of Acanthaceae which has terminal inflorescences and dies down is *Cosmianthemum*; it is unusual in having somewhat fleshy roots; otherwise the roots of these forest herbs are thin and wiry.

By no means all the dicotyledons with axillary flowers become decumbent at the base. A very frequent habit is a stiff erect unbranched stem with the leaves tending to be in the upper part, sometimes in a distinct cluster near the top — rather the habit of a miniature palm tree. Once again we have no knowledge of the duration of such plants. This habit is found in a number of genera, for instance *Didymocarpus*, *Didissandra* and *Cyrtandra* (Gesneriaceae), *Sonerila* (Melastomaceae) and *Neckia* (Ochnaceae).

A simple modification is found when species grow horizontally from vertical cliff faces; then the terminal tuft of leaves is eccentric, the leaves on the lower side being longer; in *Cyrtandra mirabilis* C.B.Cl. the longest leaves may be as much as

70 cm, and as they are thin and delicate this would be an impossible size on an erect stem. In this habitat, too, is found an elaboration of the simple pattern; the stem is branched, each branch having its characteristic tuft of leaves: in a form of *Didymocarpus gracilipes* C.B.Cl. there may be as many as 20 leaf-tufts. Again it is difficult to envisage this pattern being successful as an erect stem. Cliff-plants with these fans of pendulous leaves are found in both Asiatic and American Gesneriaceae (cf. *Resia* H. E. Moore, 1962), and also in such genera as *Steenisia* (Rubiaceae).

Another variant is the plant with an erect fan of leaves sometimes found on steep slopes and banks in the forest. Here the stem is short, or the lower part becomes prostrate keeping the leaf tuft near ground level. Such a fan of leaves, each about 30 cm long, is beautifully shown in *Cyrtandra penduliflora* Kraenzl. and is associated there with marked anisophylly—one leaf of each pair is reduced to a small stipule-like structure — and the development of prop roots, perhaps 20–30 cm long and 2 mm diam. quite rigid and branching only when they have reached the soil. These are of obvious value in supporting the plant in steep habitats.

It might seem that the simple erect stem and the decumbent, branched, patch-forming type stand widely apart. However, *Didymocarpus malayanus* Hook. f. is a plant of the Malay Peninsula which occurs in two forms: one has an erect unbranched stem, but the leaves show rather less apical aggregation than characteristic of that pattern, while the other is a prostrate mat-forming type, the shoots never being more than about 6 inches above the surface of the ground. Although the inflorescences of the erect plant carry many more flowers, there appears to be no essential difference between the two: if eventually separable as distinct species, they are at least very closely allied.

One noteworthy type of growth that I have not personally encountered in Sarawak (and I think it is not recorded there) is the much branched monocarpic herb represented by several species of *Strobilanthes* (Acanthaceae). These plants are well known for their gregarious habit and their periodic simultaneous flowering. Records for Sumatra and Java are summarized by van Steenis (1942); they include *S. kunthianus* Benth. from open grassy places and *S. cernuus* Bl. and others which are "hygrophytes of rather dark mountain forests". The habit is best known in species of *Strobilanthes* found in the seasonal forests of India, and also occurs in other genera of Acanthaceae (*Isoglossa*, *Mimulopsis*) in the evergreen but distinctly seasonal forests of eastern and south-eastern Africa.

In these seasonal forests underground storage organs become much more frequent in dicotyledons: climbers with annual stems and tubers become prominent (*Gerrardanthus*, *Cissus fragilis* Harv., *Tacazzea* in Natal) and genera which lack storage organs in rain-forest, or in the always-damp habitats in these seasonal forests, develop them: for instance *Begonia*. In south-east Africa *Impatiens duthieae* L. Bolus is found in always-damp situations in the forest and has no storage organs, *I. flanaganiae* Hemsl., more exposed to seasonal change at the forest margin, has tubers; in northern Malaya *Impatiens mirabilis* Hook. f., a plant of the somewhat seasonal forests on the limestone, has a thickened storage trunk resembling an *Adenium*.

Two genera of monocotyledons that range from the seasonal monsoon forests of south-east Asia down into the rain-forest are particularly interesting. These are *Arisaema* (Araceae) and *Hedychium* (Zingiberaceae). By far the greater number of the species of *Arisaema* live under markedly seasonal conditions: they have an underground corm which produces leaves and inflorescence annually and has a distinct period of rest. This pattern is found also in *Arisaema fimbriatum* Mast. of the Langkawi Islands, N. Malaya, where the forest is largely evergreen, but with a proportion of deciduous species and a distinctly dry and cool winter. Species are found further south on the mainland (*A. anomalum* Hemsl.) and in Borneo

and Java (*A. umbrinum* Ridl., *A. filiforme* Bl. etc.), which have a thick fleshy rhizome, rather than a corm, and these plants have leaves present all the year round. *Hedychium* is rhizomatous throughout its range, but in the northern seasonal area all the leaf fronds die down in winter and the plant is dormant; in the Bornean *H. cylindricum* Ridl. there are leaf fronds present throughout the year.

Another aroid, *Amorphophallus*, seems to be somewhat anomalous in its behaviour. It has a large corm and Walter (1971, p. 118) reports that in Africa, where it grows in seasonal areas, it flowers before it leaves. In Sarawak, where it is by no means uncommon, a corm will produce a flower in one year, a leaf in another: adjacent corms are in growth simultaneously so that flowers and leaves may be found together. However there is probably no strict alternation of flowering and leafing years: it seems likely that flowering only takes place at intervals of several years; one can see 50 plants in leaf for every one with an inflorescence. In any case *Amorphophallus* is, I think, unique among the rain-forest herbs in having a well-marked annual dormancy.

To return to the comparison of monocotyledons and dicotyledons, we find that rhizomes and stolons with scale leaves are virtually restricted, in the rain-forest, to the monocotyledons. The dicotyledons lack subterranean, or superficial, shoots with scale leaves and diageotropic growing points. As these features are well known amongst the dicotyledons of temperate forests, it is reasonable to suppose that they have been developed there in response to a markedly seasonal climate. In the monocotyledons they seem to be part of the normal developmental pattern of the plants: their well developed scales represent only the sheaths of the mature leaf and remind us that in the monocotyledons the sheath is a much more important part of the leaf than it is in the dicotyledons, where it is well-developed only sporadically in quite diverse families (Umbelliferae, Polygonaceae etc.). The important role of the rhizome in monocotyledons is perhaps another aspect of growth linked to their fundamentally hypogeal pattern of germination (cf. Burt, 1972).

Many of the dicotyledonous herbs of the forest floor have small seeds; such are all the Gesneriaceae, *Begonia*, some Rubiaceae and a few Acanthaceae (e.g. *Staurogyne*). Such seeds are probably dispersed by rainwash or by carriage on the feet of animals, and these two methods probably provide the best chance of dispersal under rain-forest conditions. Small seeds may also be favoured by the fact that they do not offer a desirable food-store to seed-predators. Salisbury's comparative study of seed size in relation to open and woodland habitats in temperate Europe showed that amongst closely related species those of shady habitats had larger seeds. Such a comparison is scarcely possible in Sarawak where the primary vegetation of virtually the whole country is forest.

The advantages of small seeds in rain-forest, suggested above, may be enough to outweigh the limitations imposed by the seedling having to start life with a very small capital of food reserves. These limitations would, however, exert a selection pressure in favour of any seedling strategy that evaded or ameliorated them. I have suggested elsewhere (Burt, 1970) that this is just what is achieved by the continued post-germination growth of one cotyledon in Gesneriaceae. The enlarged photosynthetic surface enables the seedling to build up energy for the organization of the plumular bud, which is delayed by comparison with its rapid appearance in most plants. The fungal association formed by the roots of the microsporous orchids is, of course, another way in which this difficulty is overcome, and the same argument may be applied to a widespread dicotyledonous saprophyte of the Malesian rain-forest, *Cotylanthera* (Gentianeae). In another microsporous family of monocotyledons, Burmanniaceae, both (fully?) autotrophic (*Burmannia longifolia* Becc.) and heterotrophic species (*B. sphagnoides* Becc., etc.) are found in the forest, but here the heterotrophic association is with blue-green algae, not with fungi.

Begonia is a microspermous genus of herbs in tropical forests all over the world. It does not seem to have any means of offsetting this disadvantage of small seeds: yet although *Begonia* plants are common, and seed-setting apparently prolific, seedlings are in my experience (which I admit is inadequate) curiously rare — especially as collected seed germinates freely in the greenhouse. This, of course, is not a situation affecting *Begonia* alone. Seedlings of herbaceous plants are so uncommon in the rain-forest that very little can be said about them. However the situation is similar, but perhaps a little less pronounced, in temperate forests, so this is not a rain-forest peculiarity. Nonetheless their rarity in the very open vegetation of the forest floor is noteworthy and needs investigation.

To this seedling rarity there are a few exceptions. Seedlings of two genera of Gesneriaceae are not infrequent, sometimes very prolific, in rocky forests on limestone. These genera are *Monophyllaea* and *Epithema*. We do not know the exact duration of the normal life cycle of these plants but it is certain that in both genera it is relatively short. In other words seedlings occur plentifully when they are necessary for the maintenance of the species. We are reminded that the biennial *Digitalis purpurea* L. produces seedlings freely in European woodlands, while young plants of *Primula vulgaris* Huds. need to be carefully sought. Similarly in subtropical evergreen kloof forests near Durban, Natal, the short-lived monocarpic *Streptocarpus molweniensis* Hilliard (Gesneriaceae) produces myriads of seedlings. Thus reproduction by seed seems to present similar problems for investigation in forest herbs under a wide range of climatic conditions.

If there is one lesson to be learnt from the history of botany, it is surely that attempts to give physiological explanations of leaf-structure without adequate physiological experiment are extremely hazardous. And physiological experiments in tropical rain-forest have so far been quite inadequate both in precision and in the range of subject used. All I can do here is to abstract some current thought from the physiological literature and try to relate it to the features I have seen in rain-forest herbs. If it spurs someone to write an authoritative account I shall be more than satisfied.

Even the physical measurements of the environment are very difficult in rain-forest (cf. Schulz, 1960); however it seems probable that the following conditions often obtain near the forest-floor. There is a low or very low saturation deficit; the carbon dioxide concentration is somewhat above normal (though not as high as was at one time suggested); average light intensities are low; and the incidence and intensity of sun-flecks, leading to sudden rises in leaf-temperatures, are a factor of great physiological significance (Evans, Whitmore & Wong, 1962). In this latter connexion Evans (1972, p. 34) has emphasized the extreme complexity of leaf temperatures, the extent of changes and their effects.

As to the plants' behaviour under these conditions, the early hypothesis of Stahl (1896) has now been abandoned: it was that a high transpiration rate was necessary to permit adequate salt absorption from weak soil solutions, and he interpreted various structural peculiarities as aiding this high transpiration rate. It is now known, from greenhouse studies, that an increase in the CO₂ concentration not only enhances assimilation, but lowers the transpiration rate (Hughes 1966; Meidner & Mansfield 1968, p. 76). Plants on the forest floor actually have very low transpiration rates (McLean 1919, Walter 1971); so this feature harmonizes with the higher CO₂ concentrations found there.

Rain-forest herbs have typical shade-leaf histology in that they are thin and the palisade often consists of only a single layer of shallow cells. However a more specifically rain-forest feature is the frequent occurrence of a well-developed water-storing hypodermis, or in its absence the epidermis itself is large-celled and aqueous (for notes on *Cyrtandra* see Bokhari & Burt, 1970). It has been shown (McLean, 1919) that development of conducting tissue in rain-forest herbs is relatively weak.

One is tempted to link water storage to the sudden effects of sun-flecks on the one hand and poorly developed xylem on the other: but no experimental work in this field is known to me. Nor, as far as I am aware, has the working of stomata on raised "turrets" (common in Gesneriaceae, and see the illustration of *Ruellia* in Strasburger, 1965) been studied experimentally. Until we know how they affect transpiration when they are open, and how often they are open, speculation can only be wild.

Leaf-surface is of considerable interest amongst rain-forest herbs. Not infrequently the upper surface is thrown up into numerous small peaks with corresponding hollows below; this is the condition usually described as "mammillate". It occurs, at least, in some species of *Cyrtandra* and *Didymocarpus* (Gesneriaceae), and *Begonia* (Begoniaceae), and in Tropical America species of *Pilea* (Urticaceae) show the same feature. The palisade tissue is continuous over these peaks and thus its quantity is increased within a given leaf area. Although the direct incident light on that area remains the same, it may be that this type of surface permits the plant to make better use of the lateral component of the lighting. It would be interesting to compare the assimilation of smooth and mammillate leaves when direct illumination is excluded.

Another well-known feature of certain plants growing in deep forest shade is their blue-green iridescence. Lee & Lowry (1975) have recently returned to a study of this phenomenon and now suggest that the iridescence is produced by a structural layer in the wall of the epidermis which increases the reflection of light rays in that part of the spectrum that is of least value in photosynthesis, but enhances the penetration of the most useful wavelengths. *Selaginella* is probably the commonest plant showing this iridescence, but it is also found in flowering plants such as *Begonia* and is very well-marked in *Mapania* (Cyperaceae).

Leaf colour in forest herbs is a subject that has attracted much speculation; but I have not found much detailed information in the literature on its occurrence. The phenomena generally discussed are red coloration in general and red-green or silver-green mottling; adaptive advantages have been sought for these conditions. It is therefore worthwhile to put on record that any advantage that they do confer on the plant has often been inadequate for them to become constant within the species concerned. For instance, closely adjacent or mixed populations of *Sonerila tenuifolia* Bl. (Melastomataceae) may be found with green or purple leaves, either colour being with or without whitish blotches; some *Begonia* species occur in colonies showing a mixture of blotched and unblotched leaves; *Sonerila borneensis* Cogn. may have leaves of plants growing within a short distance of one another silver-streaked or plain green, and the same applies in *Monophyllaea glauca* C.B.Cl. var., in which silvering, when present, is more conspicuous in the seedling phase. Similarly in *Cyrtandra splendens* C.B.Cl. plain green leaves, leaves mottled in darker and lighter green, leaves flushed or wholly coloured red on the underside or leaves red on both surfaces seem to occur indiscriminately. It is also well known that some 'forms' of the species popular for greenhouse cultivation have leaves more spectacularly coloured than others (e.g. cultivars of *Episcia reptans* Mart. — Gesneriaceae — and *Bertolonia* — Melastomataceae). Little emphasis has been placed on the implication of intraspecific variation when considering the possible adaptive significance of these colour patterns. This is not to deny that they may be adaptive, and in some species (e.g. in *Dossinia marmorata* Bl., or in the light and dark green mottling of many species of *Paphiopedilum*, both Orchidaceae) they do seem to be constant. But the examples of inconstancy within a species are too frequent to be ignored.

One thing is clear in this physiological uncertainty: that the forest-floor environment in evergreen tropical forest is far from optimal. Richards (1952, p. 98) has emphasized this, and points to the relatively low number of families represented in the herbaceous flora. It will have been noted how often the genera *Begonia*, *Cyrtandra*, *Didymocarpus*, *Argostemma*, *Sonerila* have recurred as examples; this is partly due to my limited experience but it does also demonstrate that these large genera have shown parallel evolutionary diversification to cover several successful growth-forms. There is scope for an interesting study in assessing how many groups of genera have representatives in, or are wholly confined to, the herbaceous flora of the rain-forests and the extent of their diversification there.

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